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Subiculum, Presubiculum, Parasubiculum and Dentate Gyrus of The Rat Brain – Cyto- and Chemoarchitectonics

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Abstract

The subiculum is still an understudied part of hippocampal pharmacy. According to histological terminology, the following layers are distinguished in the subiculum: molecular, pyramidal, multiform, perforating tract, tray, commissure of the arch, layers of dorsal and ventral fibers. In the presubiculum there are molecular, outer and inner small pyramidal, reticular, pyramidal and multiform layers. Parasubiculum contains molecular, pyramidal and multiform layers. II, the main layer, is formed by the perikarya of large pyramidal neurons. The dentate gyrus (parahippocampus) in the anterior part of the brain is located under the hippocampus proper, and in the posterior part it is medial to it. It consists of three layers. There are 9 types of neurons in these layers. The data presented in the article can serve as a fundamental basis for further study of the parts of the rat brain in normal and pathological conditions with further extrapolation of the obtained data to humans.

Keywords: subiculum; presubiculum; parasubiculum; dentate gyrus; hippocampus

Subiculum

The subiculum is still an understudied part of hippocampal pharmacy (Figure 1).

According to histological terminology, the following layers are distinguished in the subiculum: molecular, pyramidal, multiform, perforating tract, tray, commissure of the arch, layers of dorsal and ventral fibers. The first three layers contain the perikarya of neurons, while the underlying ones contain their processes [8]. The main neurons of the subiculum are large pyramidal neurons [3].

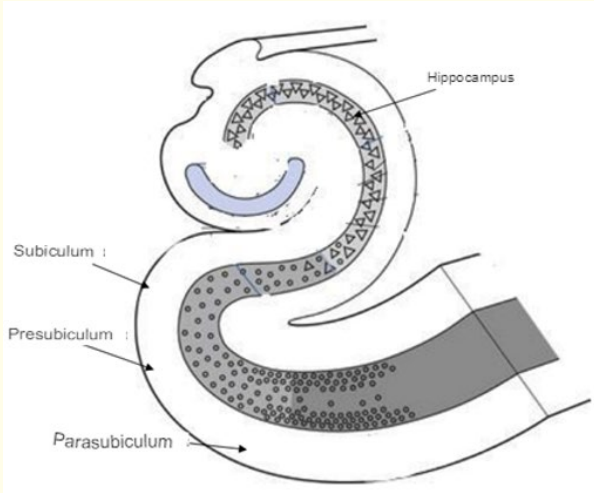

Figure 1: Location of the subiculum, presubiculum and parasubiculum of the rat brain (according to the US National Library of Medicine).

These cells are relatively uniform in shape and size, with apical dendrites extending into the molecular layer, while basal dendrites are located in deeper areas of the pyramidal layer [11].

The interneurons of the subculum are basically similar to those in the hippocampus proper. Their neurotransmitters are GABA, somatostatin and parvalbumin (table 1).

Name of the neuron	***Cortical layers***	***Mediator***
Non-pyramidal interneurons	molecular	GABA, somatostatin, parvalbumin
Non-pyramidal interneurons	multiform	GABA, somatostatin, parvalbumin
pyramidal neurons	pyramidal	acetylcholine
Basket neurons	pyramidal	GABA
Candelabra cells	pyramidal	GABA

Table 1: Neuronal and transmitter organization of the subiculum.

Interneurons form synaptic connections with the fibers of the perforating pathway.

Information about subicular projections is contradictory. A combined electrophysiological and neuroanatomical study made it possible to establish afferent and efferent connections between the neocortex and the subiculum. However, other neuroanatomical studies have not confirmed this. At the same time, the connections of the subiculum with subcortical structures have been studied in sufficient detail.

Afferent fibers from the septal complex and the nucleus of the medial septum nucleus form synapses with neurons of the pyramidal and molecular layers. Afferents of the caudomedial parvicellular basal nucleus, paraventricular nuclei, and nuclei of the thalamus go to the molecular layer of the subiculum [5, 12].

The subiculum forms efferent connections with the medial part of the prefrontal cortex [10, 12], the agranular part of the retrosplenial cortex (layers II-IV) [7, 13], the anterior olfactory nucleus, the nuclei of the hypothalamus, and the septal complex.

Presubiculum

In the presubiculum (Figure 1) there are molecular, outer and inner small pyramidal, reticular, pyramidal and multiform layers [3, 14].

The fine pyramidal layers consist of small, dark Nissl-stained neurons. In the outer fine-pyramidal layer, they are located more densely than in the inner one. Layers II, III and IV, in addition to the pyramidal ones, also contain stellate GABAergic neurons, the apical dendrites of which reach the molecular layer [9, 14] (2).

Name of the neuron	*Cortical layers*	*Mediator*
Brake non-pyramidal interneurons	molecular	GABA, parvalbumin
Exciting non-pyramidal interneurons	molecular multiform	calretinin
Pyramidal neurons	external and internal small pyramidal, pyramidal	acetylcholine
Basket neurons	external and internal small pyramidal, pyramidal	GABA
Candelabra cells	external and internal small pyramidal, pyramidal	GABA
Star-shaped neurons	external and internal small pyramidal, pyramidal	GABA

Table 2: Neural and transmitter organization of the presubiculum.

Inhibitory interneurons are located in the superficial layers, forming axon baskets around the bodies of pyramidal neurons; their mediators are GABA and parvalbumin; they are found only in the dorsal part of the presubiculum. Calretinin-positive interneurons of the multiform and molecular layers are excitatory [9, 14].

Electrophysiological studies have shown that the neurons of the surface layers have pronounced monosynaptic effects on the neurons of the deep layers, while there is practically no feedback. The presumbulum forms bilateral synaptic contacts with the subiculum, the fields of the hippocampus, the molecular layer of the dentate gyrus, and the entorhinal cortex (mainly layer III) [1, 15].

Afferents go to the presubiculum from the retrosplenial cortex of the dorsal part of the medial prefrontal cortex [7, 13, 15], the dorsal nuclei of the thalamus, the endopyridian nucleus, and the nuclei of the hypothalamus.

The efferents of the presubiculum form the axons of the pyramidal neurons. Basically, they form connections with the granular retrosplenial cortex [7, 13] and the nuclei of the thalamus.

Parasubiculum

Parasubiculum (Figure 1) contains molecular, pyramidal and multiform layers [3]. II, the main layer, is formed by the perikarya of large pyramidal neurons. In addition to them, there are candelabra cells and basket neurons, which have an inhibitory effect on pyramidal neurons. Layers I and III consist of inhibitory GABAergic and excitatory calretinin-positive non-pyramidal interneurons [9, 16] (Table 3).

Name of the neuron	*Cortical layers*	*Mediator*
Brake non-pyramidal interneurons	molecular	GABA,parvalbumin
Exciting non-pyramidal interneurons	Molecular multiform	calretinin
Pyramidal neurons	pyramidal	acetylcholine
Basket neurons	pyramidal	GABA
Candelabra cells	pyramidal	GABA

Table 3: Neuronal and transmitter organization of the parasubiculum.

Afferents to the parasubiculum come from the hippocampus, subiculum, dentate gyrus, entorhinal cortex [1], amygdala, and thalamus. Basically, they form synapses on neurons of the molecular and pyramidal layers.

Efferent fibers formed by the axons of pyramidal neurons form connections with the hippocampus, presubiculum, and entorhinal cortex (mainly layer II).

Dentate gyrus

The dentate gyrus (parahippocampus) in the anterior part of the brain is located under the hippocampus proper, and in the posterior part it is medial to it. It consists of three layers. The deepest on the frontal sections is the molecular layer (stratum moleculare), then the granular layer (stratum granulare), and the uppermost is the multiform layer (stratum multiforme) [2, 3]. There are 9 types of neurons in these layers.

In the molecular layer are the bodies of small basket neurons, whose axons end on the basket cells of the granular layer, and the dendrites do not leave the molecular layer. The second type of neurons in the molecular layer are candelabra cells. Their axons go to the granular layer, and dendrites branch within the molecular layer. These types of neurons receive impulses through the excitatory perforant pathway, are GABAergic (they also contain parvalbumin), and have an inhibitory effect on granular neurons [18]. In addition, this layer contains dendrites of granular, basket and polymorphic neurons [11, 17] (Table 4).

Name of neuron	***Cortical layer***	***Mediator***
Basket neurons	molecular	GABA, parvalbumin
Candelabra cells	molecular	GABA, parvalbumin
Granular neurons	granular	glutamate, dynorphin
Basket neurons	granular	GABA, parvalbumin
Bryophyte neurons	polymorphic	GABA
Fusiform neurons	polymorphic	GABA
Small polymorphic neurons	polymorphic	GABA
Stellate neurons	polymorphic	GABA
Candelabra cells	polymorphic	GABA

Table 4: Neural and transmitter organization of the dentate gyrus.

There are 2 types of neurons in the granular layer [17]. Granular neurons have elliptical perikarya. The branches of their dendrites are directed to the molecular layer. Between granular and polymorphic neurons are basket cells. Their axons entwine the perikarya of granular cells, apical dendrites go to the molecular layer, and basal dendrites go to the polymorphic one. Granular neurons use glutamate and dynorphin as mediators, while basket neurons use GABA and parvalbumin. Of particular importance is the fact that neurons in the granular layer continue their differentiation in adult rats.

There are five types of neurons in the polymorphic layer. The most common of them are mossy. Their perikaryons are pyramidal or polygonal in shape. Dendrites form branches within the polymorphic layer, and axons terminate on other neurons of the same layer and on the pyramidal neurons of the hippocampal fields. In addition to moss cells, there are spindle-shaped, small polymorphic, stellate neurons, and candelabra cells [17].

They receive afferent innervation from mossy fibers, and their axons either form synapses within the polymorphic layer or extend into the fields of the hippocampus, to its pyramidal neurons. All neurons of the polymorphic layer contain the GABA mediator and have an inhibitory effect on the pyramidal cells of the hippocampal fields and on neighboring neurons of their own layer.

There are two main types of neuronal circuits in the hippocampus: trisynaptic and monosynaptic [19]. In the trisynaptic circuit, afferent innervation comes from the entorhinal cortex and enters the granular neurons of the dentate gyrus through the perforating pathway (it perforates the subiculum). Axons of granular neurons form mossy fibers and form synapses with dendrites of CA3 pyramidal neurons [20]. From CA3, impulses are transmitted to CA1 and CA2 by Shaffer fibers (axons of CA3 pyramidal neurons). The axons of pyramidal neurons CA1 form an efferent feedback with the entorhinal cortex through the subiculum [1, 4, 6].

The monosynaptic circuit, bypassing the dentate gyrus and field CA3, transmits information directly from the entorhinal cortex to pyramidal neurons CA1 [6] (Figure 2).

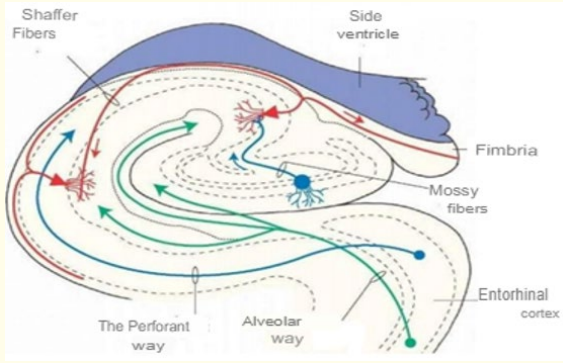

Figure 2: Diagram of pathways in the rat hippocampus (according to the US National Library of Medicine).

The data presented in the article can serve as a fundamental basis for further study of the parts of the rat brain in normal and pathological conditions with further extrapolation of the obtained data to humans.

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